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AN EXTRAORDINARY ANT-GUEST.[1]

WILLIAM MORTON WHEELER.

SINCE Sir John Lubbock's discovery of the association of certain Phoridæ (*Phora formicarum* Ver. and *Platyphora Lubbocki* Ver.) with ants,[2] several interesting additions to the number of known myrmecophiles and termitophiles belonging to this family of Diptera have been recorded. Among others a singular group of wingless Phoridæ ("Stethopathidæ") has been described by Wasmann[3] from specimens captured in the nests of termites, and Brues has recorded the occurrence of several somewhat similar forms in the nests of certain Texan ants belonging to the genera Eciton and Solenopsis.[4] Very recently Pergande[5] has published an entertaining note on the habits of a phorid (*Apocephalus pergandei* Coq.) which causes the workers of the common wood-ant (*Camponotus pennsylvanicus*) both figuratively and literally to "lose their heads," for the interior of this important portion of the ant's body furnishes the fly-larva with food and a retreat for pupation.

Far less injurious to its hosts is a myrmecophilous phorid which I propose to describe in the following pages. Unfortunately I have seen only its larval and pupal stages, but these are passed under such unusual circumstances that the discovery of the imaginal insect could scarcely supply details of very great additional interest. As the insect is not very common, many months may pass before I am able to complete my study of its life history. There is some excuse, therefore, for publishing these fragmentary observations.

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[1] *Contributions from the Zoölogical Laboratory of the University of Texas*, No. 23.

[2] Lubbock, Sir John. *Ants, Bees, and Wasps.* 1881.

[3] Wasmann, E. Termitoxenia, ein neues flügelloses, physogastres Dipterengenus aus Termitennestern, *Zeitschr. f. wiss. Zool.*, Bd. xlvii, No. 4 (1900), pp. 599–617, Taf. XXXIII.

[4] Brues, C. T. Two New Myrmecophilous Genera of Aberrant Phoridæ from Texas, *Am. Nat.*, vol. xxxv, No. 413 (May, 1901), pp. 337–356, 11 figs.

[5] Pergande, Theo. The Ant-decapitating Fly, *Proceedings Ent. Soc. Wash.*, vol. iv, No. 4 (1901), pp. 497–502, 2 figs.

On October 27 of last year I made a short excursion to Mt. Barker, which is hardly more than an hour's walk from the university at Austin, Texas. The woods about the base and on the slopes of the elevation are favorite nesting grounds for the large black ponerine ant, *Pachycondyla harpax*. In October this ant is rearing its second brood of larvæ and pupæ, having completed the education of its first brood during June and July.[1] Wishing to continue some observations on the habits of Pachycondyla, I dug up one of the largest nests I could find and carried it home in a bag. On transferring it to a Lubbock nest I took the census of the colony and found it to comprise 25 worker ants, 13 cocoons, 8 mature larvæ, 7 immature larvæ, and a packet of eggs. While counting the larvæ, which are shaped like the well-known cucurbitaceous product known as the "crook-necked squash," and covered with hairy tubercles, I noticed that six of the largest and one of the smallest presented an unusual appearance. Each of these seemed to wear about its neck a huge collar, — a sort of Elizabethan ruff, — consisting of a curled larva. That this could not be another ant-larva was apparent from a moment's examination. In all cases it almost completely encircled the ant-larva in the region of the first abdominal, or in some cases the metathoracic, segment. The posterior end was provided with a sort of disk, which adhered so tightly that both larvæ could be killed in alcohol without separating. The collar-like larva was broad behind the middle, but tapered anteriorly to a very slender thoracic region and head provided with small jaws. These were supported by a chitinous frame-work of such characteristic structure as to show that the adult form must be a true dipteron fly. The very smooth and tense integument, which was armed with some short, hooked bristles, was very transparent, so that the peristaltic movements of the viscera were clearly visible. One of the adult Pachycondyla larvæ with its living collar is shown in Fig. 1.

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[1] For an account of the habits of this ant, see my paper, A Study of Some Texan Ponerinæ, *Biol. Bull.*, vol. ii, No. 1 (Oct., 1900), pp. 1–31, Figs. 1–10.

As soon as the ants had been transferred to the Lubbock nest they were given a number of young larvæ of *Camponotus sansabeanus*. These they soon proceeded to malaxate with their mandibles, twirling the morsels about in the mean time with their fore legs and lapping up the exuding juices with their tongues. Finally they deposited the crumpled and pulpy remains of the Camponoti on the trough-like ventral surfaces of their larvæ, which had been previously placed on their backs in a rough chamber dug in the earth of the nest. This chamber was immediately under the glass roof-pane, so that further developments could be closely observed with a pocket lens. Each ant-larva at once stretched forth its head eagerly and began to devour the viands with which it had just been provided. At the same moment the dipteron larva, too, as if sniffing the odor of the fresh food, unwound its tapering neck from the ventral surface of its host, and, without shifting the attachment of its posterior end, at once plunged its mandibles into the food. Under the lens both larvæ could be seen greedily dining side by side till the last particle of the Camponotus larva had been consumed or prematurely removed by the worker ants.

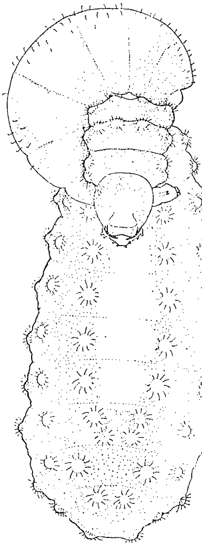
Fig. 1. — Adult larva of *Pachycondyla harpax* bearing a commensal phorid larva.

When the ant-larvæ were huddled close together, a collar-like larva was sometimes observed to reach over and help itself from the food supply of a neighbor; but even when thus compelled to crane its neck to the utmost, it never shifted the attachment of its caudal end. Sometimes when there was no food within reach it would tweak with its sharp little jaws the sensitive hide of a neighboring ant-larva, till the latter squirmed with pain. It would sometimes even tweak its own host, as if to make it wriggle and perhaps thereby incite the worker ants to bring a fresh supply of provisions.

The following day two living myriopods (Lithobius) were placed in the nest. During the morning hours they were killed by the Pachycondyla workers, shorn of their many legs, cut up into pieces of convenient length, malaxated, and fed to the larvæ as on the preceding day. And again I was able to witness the strange banquet — the dwarf reaching down from the shoulders of the ogre and helping himself from the charger formed by the trough-like belly of his host. The same observation was repeated on several successive days. Pieces of various ant-larvæ, beetle-larvæ, Lithobius, Scutigera, Oniscus, — all were served up to the ant-larvæ and partaken of with great relish by the dipteron larvæ as well. There could be no doubt that the latter were true commensals, — perhaps the most perfect commensals, in the original meaning of the term, to be found in the whole animal kingdom

As one of the smallest Pachycondyla larvæ, scarcely one-fourth grown, bore a very small dipteron larva, it is, perhaps, safe to say that the ant-larva acquires its commensal at a very early age. The two then grow up together, so that there is always a certain relation between the two kinds of larvæ — large Pachycondyla larvæ bearing large commensals, and *vice versa*. The worker ants lick and cleanse the commensals at the same time that they are caring for their own larvæ. This is usually done just after meals. Since, during this operation of cleansing, the ants spend no more time over the commensals than they do on a similar area of the body surface of their own larvæ, it would seem that they are not even aware of the existence of the commensals. To these nearly blind ants, which must rely almost exclusively on their senses of touch and smell, the larvæ bearing commensals, if distinguished at all from individuals without such attendants, would probably be perceived merely as having unusually protruding necks. But there is nothing to indicate that these insects are really capable of perceiving such differences in their environment.

At this time an amusing interlude in these observations was furnished by introducing into the nest a few living "pill-bugs" (Armadillidium sp.). For two whole days the Pachycondyla workers hunted these isopods from one corner of the nest to another. An Armadillidium would scurry along rather quickly and, when overtaken, escape death by rolling itself up into a hard ball, which the ants tried in vain to perforate with their mandibles. As soon as they desisted the Armadillidium would unroll itself, and the chase would begin again. Finally I was compelled to remove the crustaceans, as the larvæ seemed to be in danger of being injured in the excitement of the chase.

On the 5th of November I obtained satisfactory evidence that the dipteron larva is not obliged to remain always with the same Pachycondyla larva. During the night one of the large larvæ had moved and attached itself to the first abdominal segment of an ant larva which already bore a commensal around its metathoracic segment. The two larvæ were oriented in opposite directions, *i.e.*, with their heads reaching around opposite sides of their host. Subsequently one of these commensals moved to an unoccupied Pachycondyla larva. I was not present when the change occurred, nor was I able to determine whether it was the originally stationary or the adventitious larva that moved. Although this observation makes it certain that the dipteron larvæ can shift their position from one host to another, I am convinced, nevertheless, that they must do this with great reluctance and only under urgent circumstances, such as extreme hunger, the death of the larva to which they are attached, or, perhaps, when fully mature and about to pupate.

As the days passed, the mature ant-larvæ spun their brown cocoons one by one, and one by one the mature commensals disappeared. Did they also pupate and for this purpose conceal themselves in the soil of the nest? or had the ants at last detected the villains and converted them into food for the larvæ which had not yet pupated? or did they stick to their hosts and pupate within the cocoons? In order to ascertain, if possible, the true state of affairs, I transferred the whole colony to a fresh nest and examined the soil of the old nest with great care. There were no traces of the missing commensals. The only remaining resource was to open the cocoons. Several of the cocoons which had been taken with the nest October 27 had hatched, but by November 10 there were still thirteen cocoons in the nest, as several of the larvæ had pupated in the mean time. Five of these were opened, and in two, which contained pseudonymphs of Pachycondyla and were, therefore, of recent formation, commensals were found! Having shared the table of their host, they had come to share its bed as well. The dipteron, too, had pupated after the manner of its kind — forming a puparium; *i.e.*, instead of spinning a cocoon like the ant-larva, the dead larval skin, somewhat shriveled and contracted, was used as an envelope, and within this the pupa proper was formed.

This puparium, represented in Fig. 2, is from 2.25 to 2.5 mm. long and clearly of the cyclorhaph type. It is elliptical, much flattened dorso-ventrally, especially along the edges, which are thin and hyaline and almost alate. The brownish dorsal surface is thrown into delicate and irregular transverse wrinkles. Anteriorly, in the thoracic region, there is a pair of short black respiratory tubes. The ventral surface is very glabrous and distinctly paler than the dorsal surface. From its small size, cyclorhaphous character, and resemblance to the puparium of a typical Phora bred by one of my assistants, Mr. C. T. Brues, from some spider's eggs, I conclude that the insect under consideration must be one of the Phoridæ.

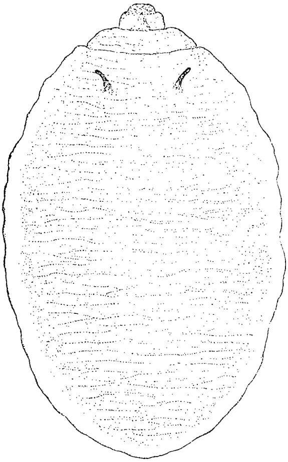

FIG. 2. — Puparium of phorid commensal from the cocoon of *Pachycondyla harpax*.

Subsequently, several other cocoons were opened and two more were found to contain the puparia of commensals. In all four cases the puparium was invariably located in the caudal pole of the cocoon, just to one side of the black blotch of ejecta deposited by the ant-larva before becoming a pseudonymph. At this point the puparium was immovably stuck to the wall of the cocoon by means of its smooth ventral surface. Its anterior end was directed towards the cephalic pole. As there is always considerable space, especially at the posterior pole, between the walls of the cocoon and the enclosed ant-pupa, the much-flattened fly puparium did not in the least crowd its host.

Reflection shows that the position of the puparium in the posterior pole of the cocoon, though the reverse of the position of the larval commensal with respect to its larval host, is the only one which can be maintained by the commensal with perfect safety. Like other ants, the Pachycondyla leaves its cocoon through a rent in the anterior pole. This rent is certainly made by the mandibles of the hatching ant, and it is possible that the callow insect may succeed in making its way out of the cocoon without any assistance from the workers. I have hitherto failed, however, to surprise one of these ants in the act of hatching. But even if the obstetrical aid of the workers is necessary, as it is in the more highly specialized Camponotinæ, any position for the commensal puparium, except at the posterior pole of the cocoon, might be fatal, for the struggling jaws and legs of the emerging ant and the jaws of the assisting ants would certainly be very liable to cut into any delicate object attached to the anterior or median walls of the cocoon. This danger, of course, would not exist if the fly hatches before the ant and is able to perforate the cocoon and escape. It is altogether more probable, however, that the ant hatches before the fly in the manner suggested below.

It would be interesting to know what the commensal larva is doing while the ant-larva is weaving its cocoon. Does it move about to avoid the swaying jaws of the spinning larva? or does it take up its position from the first at the posterior end of the larval ant and there remain motionless while the posterior pole of the cocoon is being completed? It is very difficult to answer these questions. The fact that the posterior poles of all the cocoons containing puparia were somewhat distorted, being broader, more obtuse, and more irregular than the normal cocoons, would seem to indicate that the ant-larva may modify this end of its cocoon for the better accommodation of the commensal. I am inclined to believe, however, that the distortion may be produced by the dipteron larva while attaching itself just before pupating to the newly woven and still plastic cocoon.

At this point my observations end. The phorid puparia were kept for several weeks in what I supposed to be the proper conditions of warmth and moisture, but to my intense disappointment they failed to hatch. During the autumn and winter frequent and diligent search was made for more of the commensals in all the Pachycondyla nests I could find, but in vain. Finally, during the latter part of May of the current year, I discovered in a very different locality two Pachycondyla nests which contained a few phorid larvæ. This discovery proved that the phorid is double-brooded like its host. But the larvæ were very small and attached to such very young ant-larvæ that I despaired of being able to raise them in my artificial nests as far as the imaginal stage. It remains, therefore, for the future to fill this gap in my observations.

As a small contribution towards filling this gap I venture to advance the following conjecture concerning the circumstances under which the phorid fly probably hatches. I assume that the ant must hatch before the fly. Now very soon after the former hatches the useless cocoon is always carried by a worker and placed on the refuse heap, which in the natural nest is often almost entirely made up of the empty cocoons of from one to several broods of ants, and lies in a rather dry and well-ventilated spot immediately beneath the stone covering the nest. Along with the cocoon is carried the phorid puparium still adhering to the wall at its unopened posterior end. Thus after a privileged existence as free pensioner and bedfellow to a generous host, it is unwittingly carried away in the worn-out bedclothes and consigned to the family rag pile. Here the small and probably very active fly hatches, leaves by the wide-open front door of the cocoon, and, after mating, either returns to lay a few eggs in the galleries of its former host, or flies away to oviposit in some other Pachycondyla nest. Thus the simple assumption that the fly hatches later than the ant renders it unnecessary to suppose that the fly possesses some peculiar means of perforating the tough wall of the cocoon, and also accounts for the position of the puparium in the posterior pole, where it would be completely concealed from the workers even after the escape of the callow ant.

In conclusion the reader's attention may be directed to certain particulars of special interest in connection with the life history of the Pachycondyla commensal:

First, the peculiar habits of the phorid show clearly that the ponerine method of feeding the larvæ with comminuted insects is not only the typical but the only method employed by these ants, for such a commensal would certainly starve if the Pachycondyla larvæ were carefully fed like the larvæ of Camponotus and Formica, by regurgitation of liquid food from the mouths of the workers. The phorid profits by a peculiarity in the behavior of its host, and thereby demonstrates — by one of Nature's experiments — that *Pachycondyla harpax* cannot feed its young by regurgitation.

Second, in the peculiar symbiotic relationship existing between the phorid and the ants, the adaptations are all on the part of the former, whereas the latter pursues its ancient and well-established mode of life uninfluenced by and apparently in complete ignorance of the very existence of its little guests. Even the distortion of the cocoon may be due, as I have suggested, entirely to the activity of the phorid. These strikingly unilateral adaptations are probably to be explained on the ground that the phorid in the Pachycondyla nest is as careful and conservative — if such terms may be used — of the life and welfare of its host as Pergande's Apocephalus is ruthless and destructive. The small amount of food consumed by the former can hardly be a serious drain on the provisioning instincts of the Ponerinæ. The larvæ bearing the commensals were certainly as large and healthy as any others in the nest, and produced perfectly normal pupæ, which in the cases observed all lacked the imaginal disks for the wings and were therefore of the worker type. Whether the presence of the commensals by reducing the amount of food even to a slight degree could inhibit the development of queen larvæ and thereby convert them into workers, involves a problem as interesting as it is difficult to solve in the present state of our knowledge.

Third, the commensal of Pachycondyla, together with the Phoridæ mentioned in the introductory paragraph of this paper, shows that the flies of this family are well worth careful study. While the Stratiomyidæ, Syrphidæ, Midaidæ, etc., certainly make more attractive cabinet specimens and prettier monographic plates, it is very doubtful whether the life histories of most of these conspicuous Diptera can compare in interest with those of the tiny, dull-colored Phoridæ. That the study of the smaller and inconspicuous Diptera, like the Culicidæ, has been unduly neglected is clearly shown by recent medical researches on the malaria parasite.

COLEBROOK, CONN., August 16, 1901.